RESEARCH PAPER

Distinguishing between signal and noise in faunal responses to environmental change

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ABSTRACT

Aim We tested whether variation in snapshots of butterfly species composition and species richness taken from one to six years apart could be interpreted as an ecologically meaningful trend or whether they might merely reflect stochasticity.

Location Field research was conducted in the Toquima Range and Shoshone Mountains, Lander and Nye counties, Nevada, USA.

Methods We obtained data for 49 sites in the Toquima Range from 1996 to 2002 and 39 sites in the Shoshone Mountains from 2000 to 2002. Sites spanned the gradient of local topographic and climatic conditions in those mountain ranges. Data on species composition and species richness were based on comprehensive field inventories. We calculated similarity of species composition using the Jaccard index. We conducted one-factor repeated-measures analyses of variance to test whether the distribution of similarity of species composition and the distribution of mean species richness depended on the number of years between inventories.

Results In both mountain ranges, much less of the difference in species composition was attributable to turnover of species composition within sites over time than to spatial differences among sites. Annual species richness in the Toquima Range was more variable than in the Shoshone Mountains, but again far less of the variation in species richness was attributable to year than to differences among sites.

Main conclusions Despite the fact that desert ecosystems are not expected to be highly resilient to global environmental change, there may be a time lag between deterministic environmental changes and a detectable faunal response, even in taxonomic groups that are known to be sensitive to changes in climate and vegetation. Although information on species richness and similarity of species composition are among the most practical data to collect in managed landscapes, these measures may not be highly sensitive to environmental changes over the short to moderate term.

Key words Butterflies, conservation, desert, environmental change, Great Basin, species composition, species richness.

INTRODUCTION

Desert ecosystems are thought to be highly responsive to environmental changes, including shifts in temperature and precipitation, invasion by non-native species, and altered disturbance regimes (Smith *et al*., 1997, 2000; Sala *et al*., 2000). The Great Basin of western North America is a 'cold desert' that currently receives 250 mm precipitation each year, mainly in the form of winter snow. The region covers more than 425 000 km², approximately 75% of which is managed by federal and state resource agencies. Declines in species richness and changes in species composition of native plants and animals in the Great Basin are anticipated over the next century, especially if atmospheric concentrations of carbon dioxide continue to increase. For example, the non-native annual plant cheatgrass (*Bromus tectorum*) is likely to accelerate its invasion of sagebrush-steppe landscapes at the expense of native vegetation, increasing fire frequency in the process (Smith *et al*., 1987, 2000).

Growing awareness of the potential effects of climate change and expansion of non-native species has intensified efforts to understand the resilience of ecological systems at global, regional, and local levels (Parmesan *et al*., 1999; Thomas & Lennon, 1999; Easterling *et al*., 2000; Wuethrich, 2000; Thomas *et al*., 2001). Detection of faunal responses

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to long-term environmental change in the Great Basin and other ecosystems usually has been based on palaeoecological evidence. Although fossil records are incomplete for most groups of animals, species distributions during the middle to late Holocene have been inferred from remains in pack rat middens and from pollen deposits, which provide information on climate and the distribution of vegetation resources (Grayson, 2000; Davis & Shaw, 2001). Detection of faunal responses to shorter-term environmental change — on the order of years to decades — typically is based on surveys. When data such as weather records and remotely sensed indices of vegetation are available, field observations over a number of years can be compared against those data to determine whether there has been a detectable faunal response to known environmental changes (Tucker, 1979; Box *et al.*, 1989; Cramer *et al.*, 1999). Although few weather stations have been established in the remote Great Basin, and many remotely sensed data products are still in the initial stages of development, we can, nonetheless, use faunal inventory data to draw inferences about the potential responsiveness of the system to various perturbations.

In order to test whether environmental changes are modifying communities of native species, and to evaluate whether management strategies are meeting their objectives, it is valuable to monitor selected taxonomic groups across large areas and multiple years. Extensive monitoring data from areas that have not been subject to experimental treatments, for instance, increase our ability to evaluate whether changes in biodiversity measures result from the treatment or simply reflect background variability (Berry *et al.*, 1998; Link & Sauer, 1998). However, time and money for biological surveys and monitoring are limited, especially in a management context. Therefore, it is useful to examine whether 'snapshots' of species richness and composition accurately reflect longer-term patterns (Hanski, 1999; Moilanen, 2000).

From the 1970s to the early 1990s, ecologists frequently invoked island biogeography to predict how faunal distributions in the Great Basin and other montane ecosystems might respond to climate and other environmental changes (Diamond, 1975; Wilcox, 1980; Shafer, 1990; Guisan *et al.*, 1995; Boggs & Murphy, 1997). Forecasts usually have assumed that the distribution of particular vegetation zones and the animals associated with those assemblages will shift in concert (McDonald & Brown, 1992; Murphy & Weiss, 1992). The realism of the vegetation-based scenario has been questioned based on recognition that biotic responses to environmental change differ among taxa, and often occur at the species level rather than at the community level (Gleason, 1926; Huntley, 1991; Tausch *et al.*, 1993; Guisan *et al.*, 1995; Risser, 1995; Kupfer & Cairns, 1996). Thus, development of predictions related to faunal change has moved toward working directly with the taxonomic group of interest (Lawlor, 1998; Fleishman *et al.*, 1988, 2001).

Butterflies are associated strongly with both weather and vegetation (Dennis, 1993; Kremen *et al.*, 1993; New *et al.*, 1995). In addition, because invertebrates have relatively short generation times, they may respond rapidly to environmental change. Thus, butterflies may be useful for tracking how changes in various natural and anthropogenic stressors affect native fauna (Parmesan, 1996; Parmesan *et al.*, 1999). But the same attributes that link population dynamics of butterflies with deterministic environmental change, such as sensitivity to natural variation in temperature and precipitation, can complicate their application (DeVries *et al.*, 1997; Pollard *et al.*, 1998; Saether *et al.*, 2000). In a watershed on the western edge of the Great Basin, for example, annual variability had significant effects on butterfly diversity that far exceeded the effect of land cover (agricultural vs. nonagricultural) (Fleishman *et al.*, 1999a).

Here, we use up to six years of survey data from two mountain ranges in the Great Basin to examine whether variation in 'snapshots' of butterfly assemblages taken several years apart was indicative of a temporal trend. Our objective also can be framed as documentation of the apparent signal-to-noise ratio in these assemblages over time. Global assessment of biodiversity responses to an array of environmental changes benefits from data gathered at local and regional scales as well as at coarser scales (Easterling *et al.*, 2000). Because the latitudinal extent of our study area is relatively small, mean temperature at the northern end of the study area is unlikely to be substantially warmer than at the southern end. In addition, few of the species in our study system are at the edge of their geographical range (Fleishman *et al.*, 1997). Therefore, in contrast to studies by other workers that have examined distribution patterns over a much larger area (Parmesan, 1996; Parmesan *et al.*, 1999; Thomas *et al.*, 2001), we did not attempt to determine whether the ranges of individual species had expanded or contracted. Instead, we focused on variation in species richness (number of species) and species composition among sites and among years. These are the types of data that are most likely to be collected over relatively large areas and long periods of time given current and projected levels of funding for biological monitoring on public lands in the western United States. Related work has focused specifically on explaining and predicting the response of species richness of butterflies and occurrence patterns of individual species of butterflies to a suite of topographic gradients (e.g. Fleishman *et al.*, 2001, 2003b; Mac Nally *et al.*, 2003).

METHODS

Field methods

Data for our analyses were collected from 1996 to 2002 in the Toquima Range (approximate north–south boundaries

39°17′50″ to 38°29′9″) and Shoshone Mountains (approximate north–south boundaries 39°14′19″ to 38°57′32″0) (Lander and Nye counties, Nevada, USA). These two mountain ranges are separated by about 50 km and have similar regional climate, biogeographical past and ancestral biota, and human land-use histories (Wilcox *et al.*, 1986; Austin & Murphy, 1987; Grayson, 1993; Fleishman *et al.*, 2000). Inventories were conducted in 49 sites in the Toquima Range from 1996 to 1999 and in 2002. We visited 43 sites in 1996, 32 in 1997, 26 in 1998, 15 in 1999, and 28 in 2002. We conducted inventories in 39 sites in the Shoshone Mountains from 2000 to 2002 (27 sites in 2000, 39 in 2001, and 29 in 2002). Sites spanned the gradient of local topographic and climatic conditions in those mountain ranges.

We inventoried butterflies using walking transects, an established technique for temperate regions that reliably detects species presence and permits assessment of distributional trends across space and time (Pollard & Yates, 1993; Harding *et al.*, 1995). These methods have been described in considerable detail in previous publications (Fleishman *et al.*, 1998, 2000, 2001), so we present just a brief overview here. Approximately every two weeks throughout the majority of the flight season (late May through August — i.e. the period during which adult butterflies are present), using equal sampling effort per unit area, we recorded the presence of all butterfly species seen in each site. It is reasonable to interpret that a given butterfly species is absent if the area is searched using these methods during the appropriate season and weather conditions and none is recorded (Pullin, 1995; Reed, 1996). In the nearby Toiyabe Range, for example, we recorded 98% of the theoretical number of species expected under a Michaelis-Menten model (Clench, 1979; Raguso & Llorente-Bousquets, 1990; Soberón & Llorente, 1993). All sites were sufficiently large (1.5–44.4 ha) relative to the home ranges of resident butterflies in the region that the short-term presence of butterfly species in each site was independent (i.e. an individual was not recorded in > 1 site during an inventory round) (Fleishman *et al.*, 1997). Thus, measurement of species occurrence should not be confounded by movement among sites. We recorded 56 resident species of butterflies from our study sites. Complete data are available from the corresponding author on request.

Analyses

We calculated similarity of species composition using the Jaccard index, $C_J = j/(a + b − j)$, where j is the number of species found in both sites and a and b are the number of species in sites A and B, respectively. C_J approaches 1.0 when species composition is identical between sites and 0.0 when two sites have no species in common (Magurran, 1988). We refer to the number of years that elapsed between inventories as a 'time lag.' We calculated similarity of species composition for time lags of one to six years in the Toquima Range and of one or two years in the Shoshone Mountains.

We conducted one-factor repeated-measures analyses of variance to test whether the distribution of similarity of species composition and the distribution of mean species richness depended on the number of years between inventories. Individual sites were the objects that were measured repeatedly. Time lags (1, 2, ... , 6 years) were the repeated measures for analyses of similarity of species composition, and individual years were the repeated measures for analyses of species richness. We report variance components rather than *F*-values as our measure of the importance of each effect (Hoaglin *et al.*, 1991; Quinn & Keough, 2002). We used the variance components formulae of Neter *et al.* (1990). We considered the Toquima Range and Shoshone Mountains separately to account for differences in the calendar years in which inventories were conducted, as well as for potential range-specific differences in turnover of species composition and species richness.

Because not all sites were inventoried in all years, the actual sites included in each time lag treatment varied. For some sites, multiple values could be calculated for a given time lag treatment. For these sites, we calculated the mean C_J for each time lag. For example, if a site was inventoried in 1996, 1997, and 1998, the one-year time lag value included in the analysis of variance was the mean of the C_J for 1996–97 and the C_J for 1997–98 for that site. For the Toquima Range, three year-pairs (i.e. 1996–97, 1997–98, 1998–99) were included in the one-year time lag treatment, two year-pairs were included in the two-year time lag treatment, and one year-pair was included in each of the three-year, four-year, five-year, and six-year time lag treatments. For the Shoshone Mountains, two year-pairs were included in the one-year time lag treatment and one year-pair was included in the two-year time lag treatment.

RESULTS

Community similarity

In the Toquima Range, mean similarity of species composition varied relatively little among time lags of one to six years (0.43–0.49, Fig. 1a). Relatively little of the variance (12.8%) was attributable to time lag (Table 1). Most of the variance was unexplained in the model. The variance associated with differences among sites was about three times greater than that of time lag (the treatment effect) (Table 1). Thus, much less of the difference in species composition was attributable to turnover of species composition within sites than to spatial differences among sites.

In the Shoshone Mountains, mean similarity of species composition was about 0.6 for time lags of both one and two years (Fig. 1b). The variance attributable to time lag was
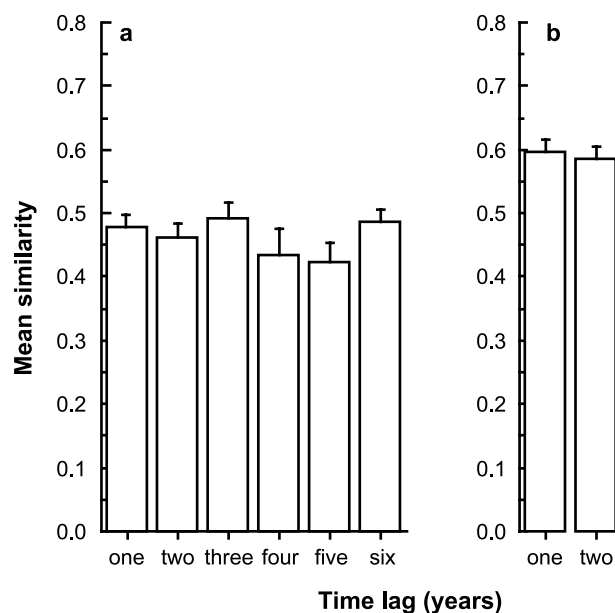
Fig. 1 Mean similarity of species composition of butterflies in (a) the Toquima Range and (b) the Shoshone Mountains, among time lags of one to six years. Error bars are standard error.

Table 1 One-factor repeated-measures analyses of variance of similarities of butterfly faunas in individual sites separated by time lags of one to six years in the Toquima Range (1996–2002) and the Shoshone Mountains (2000–02)

Source of variation	d.f.	Mean square	Variance component (%)
Toquima Range (1996–2002)			
Sites	42	0.021	31.4
Time lag	5	0.013	12.8
Residual	68	0.005	55.8
Shoshone Mountains (2000–02)			
Sites	28	0.016	73.7
Time lag	1	0.007	3.2
Residual	21	0.002	23.2

negligible (3.2%, Table 1). About three-quarters of the total variation in species composition was attributable to differences among sites.

Species richness

In the Toquima Range, there were substantial differences in mean species richness of sites among years (from 12.5 in 2002 to 18.4 in 1998) (Fig. 2a). About 26% of the variation in mean species richness was attributable to year, and about

45% was attributable to differences among sites (Table 2). Nonetheless, at the mountain range level, total species richness reached an asymptote after just two years of inventories.

In the Shoshone Mountains, mean species richness per site varied little between 2000 and 2002 (Fig. 2b). Over 7% of the variation in species richness was attributable to differences among years, while about two-thirds of the variation was associated with differences among sites (Table 2). Total species richness at the mountain range level began to approach an asymptote after the second year of inventories. The number of species recorded from the mountain range increased from 48 in 2000, to 51 in 2001, to 54 in 2002.

DISCUSSION

Whether differences in biodiversity measurements at two points in time are likely to reflect stochasticity as opposed to indicating a *bona fide* temporal trend depends in large part on two related factors: the extent of deterministic environmental change, and the degree of variability inherent in the biotic assemblage. Deserts are believed to rank among the ecosystems most responsive to environmental change (Sala *et al.*, 2000; Smith *et al.*, 2000). However, as our results demonstrate, the severity and unpredictability of environmental patterns in arid ecosystems complicates efforts to extract abiotic and biotic 'signals' from the 'noise' of background variation (Houghton *et al.*, 1975; Grayson, 1993).

We found that in the Great Basin, far less of the difference in species composition and mean species richness of butterflies over a six-year period was attributable to apparent temporal changes than to differences among sites. For example, the difference in community similarity across a six-year time lag was no greater than the difference across shorter time lags, including time lags of just one year. While these results do not rule out the possibility that species composition and species richness of butterflies have changed over time, we were unable to identify such a trend with confidence.

Temporal differences explained much less variance in species composition than did spatial differences in both of the mountain ranges that we examined. Nonetheless, we found that absolute levels of community similarity differed among mountain ranges — species composition was more similar in the Shoshone Mountains than in the Toquima Range. Similarly, while differences among years explained less variance in species richness than did spatial differences in both mountain ranges, species richness was more consistent in the Shoshone Mountains than in the Toquima Range. We obtained similar results when data were pooled among years. Species composition of butterflies — and also of birds — in the Toquima Range tends to be relatively variable compared with surrounding mountain ranges (Fleishman *et al.*, 2003a). This may reflect that the Toquima Range is more arid than other mountain ranges in its biogeographical subregion (Fleishman
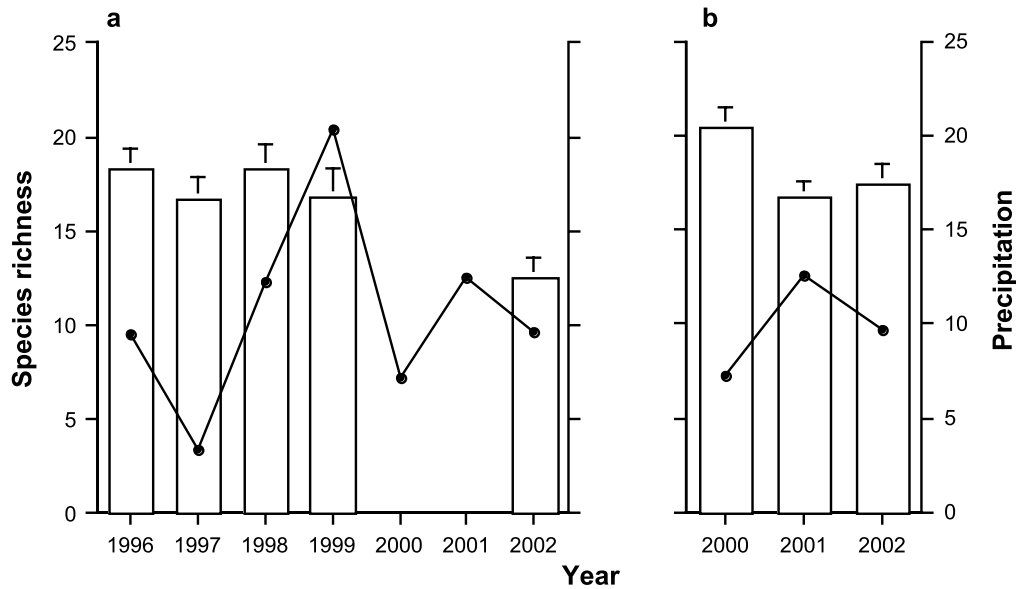
Fig. 2 Mean species richness of butterflies (□) and precipitation in cm for the year preceding the flight season (May–April) (●) in (a) the Toquima Range and (b) the Shoshone Mountains from 1996–2002. Precipitation measured in Austin, Nevada (Western Regional Climate Center, 2003). Error bars are standard error.

Table 2 One-factor repeated-measures analysis of variance of annual species richness of butterfly faunas in individual sites in the Toquima Range (1996–2002) and the Shoshone Mountains (2000–02)

Source of variation	d.f.	Mean square	Variance component (%)
Toquima Range (1996–2002)			
Sites	48	100.5	44.9
Years	4	111.2	25.7
Residual	91	11.7	29.4
Shoshone Mountains (2000–02)			
Sites	38	53.1	65.7
Years	2	28.6	7.2
Residual	49	6.4	27.1

et al., 1999b, 2000). Although the diversity of resources for butterflies (e.g. larval host plants and adult nectar sources) does not appear particularly high in either the Toquima Range or the Shoshone Mountains, field observations suggest that resources may be more limited and more patchily distributed in the Toquima Range than in the Shoshone Mountains. Heterogeneity in resource distributions may in turn correspond to variability in species composition.

Might distance between sites confound our results and interpretations? Contrary to the expectation that assemblages closer together in space should be more similar to each other than assemblages that are further apart (Underwood & Chapman, 1996; but see Underwood & Chapman, 1998), we have found that species composition of butterflies tends to be less similar among sites within a canyon than among canyons within a mountain range (Fleishman *et al.*, 2003a). Further, because we used a variance-components approach, slight spatial autocorrelation would not violate the assumptions of our statistical analyses. Including distance as a covariate in our analyses of variance might have an effect on the spatial component of variation, but would not affect our conclusions about temporal patterns.

An obvious potential explanation for the lack of a detectable temporal trend in our butterfly data is that during the relatively short duration of our study, there were few if any ecologically meaningful changes in climate or related factors such as vegetation diversity and composition. In four of the five years of our study for which data currently are available, annual precipitation fell far below the mean for the 111-year period of record (Western Regional Climate Center, 2003). In all years but 1998, annual precipitation in Austin, Nevada (roughly parallel to and equidistant from the northern end of the Toquima Range and Shoshone Mountains) was between 45% and 81% of the long-term mean (in 1998, precipitation was 155% of the long-term mean). However, precipitation from year to year was erratic — 530 mm in 1998, 160 mm in 1999, and 278 mm in 2000, for instance (Fig. 2).

We also recognize that species richness and composition may be less sensitive to environmental change than more

detailed data on abundance, reproductive phenology, interspecific interactions such as predation rates, or other demographic parameters (Parmesan *et al.*, 1999; Thomas & Lennon, 1999; Wuethrich, 2000; Thomas *et al.*, 2001). However, accurate measurement of population-level variables across many species and locations over many years can be prohibitively expensive in terms of time, money, and technical expertise. In addition, population-level data may be even more prone to random fluctuations than assemblage-level variables.

We sought not only to examine temporal patterns in butterfly assemblages *per se*, but also to elucidate the extent to which background variability in our study system could complicate detection of faunal responses to environmental change. By 2100, for example, the Great Basin is predicted to experience a 2–3 °C increase in temperature, 10% decrease in summer precipitation, and 15–40% increase in precipitation during other seasons (United States Environmental Protection Agency, 1999). As a result, snowmelt will be earlier and more rapid, leading in turn to lower groundwater tables and a reduced capacity for water storage. Dramatic biological consequences are anticipated, ranging from altered ecological function to decreases in native biological diversity and changes in species composition (McDonald & Brown, 1992; Murphy & Weiss, 1992; Grayson, 2000; Fleishman *et al.*, 2001). Yet the fauna of the Great Basin is 'tough-tested' — species with low tolerance for environmental variability probably were extirpated long ago. Furthermore, recent work has emphasized that faunal responses to environmental change may depend in part upon the speed at which those changes occur (Grayson, 2000) and the extent to which the variance in ecological conditions shifts (McLaughlin *et al.*, 2002). As a result, despite the fact that desert ecosystems are not expected to be highly resilient to environmental change (Sala *et al.*, 2000; Smith *et al.*, 2000), there may be a time lag between deterministic changes in climate or vegetation and a detectable faunal response.

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